Final Report

GENETIC DIVERSITY IN THE SPRUCE COMPLEX OF COASTAL ALASKA

Alaska Science and Technology Grant Agreement 89-1-015

- 1989 - 1993 -

by

Dr. John Alden, Forest Geneticist

Institute of Northern Forestry
308 Tanana Drive
Fairbanks, Alaska 99775-5500

A Research Project Planned, Funded and Carried Out Cooperatively by the Pacific Northwest Research Station of the U.S. Department of Agriculture - Forest Service; Citikon Forest Products - Anchorage, Alaska; Afognak Native Corporation - Kodiak, Alaska; Tatitlek Native Corporation - Cordova, Alaska; Eyak Corporation - Cordova, Alaska; the U.S. Department of Navy, Naval Facilities Engineering Command; and by the Alaska Science and Technology Foundation - Anchorage, Alaska.

June 1, 1993

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FORWARD

The withdrawal of public forests from timber harvest in the Pacific Northwest has created a timber shortage in the United States and increased the export value of saw logs from Alaska. Marginal stands of poor quality spruce from the Gulf of Alaska can now be harvested economically, affording land owners profits for improving the growth and quality of second generation forests. The purpose of Grant 89-1-015, "Genetic Diversity in the Spruce Complex of Coastal Alaska," was to determine: (1) If Sitka Spruce is genetically variable in growth and wood quality; (2) if genetic variation was reduced by "bottle neck effects" of small colonizing populations as Sitka spruce migrated from southeast Alaska around the Gulf to southwest Alaska; (3) the direction of gene flow in the spruce complex, the extent of hybridization and introgression among the species, and the effects of hybridization and introgression on tree growth and wood quality; and (4) how much growth and wood quality of seedlings and trees can be improved by artificial selection of seed parents for regeneration of harvested forests. These objectives are outlined on pages of one and two of the following Executive Summary, and pages 11 and 12 of the Technical Report. A modest increase in tree growth (ten percent), and wood quality will increase the area of commercial Sitka and Lutz (the natural Sitka and white spruce hybrid) spruce forests[1] in south central and southwest Alaska from less than five million acres at present to as much as 11 million acres, and increase employment and living standards of rural citizens.

To accomplish the objectives outlined in the Executive Summary and Technical Report, genetic variation within and among twenty-five populations from south central (Cordova, Copper River, Valdez, Mat-Su Valley and Kenai Peninsula Regions) to southwest Alaska (Afognak and Kodiak Islands) were examined biochemically for variation in protein (allozyme) frequencies (see methods on pages two and three). DNA of an additional 20 populations from Cordova to southern British Columbia was examined for evidence of white spruce hybridization and introgression in Sitka spruce. Seedlings of 45 wide-range provenances (geographic seed sources) of Sitka and Lutz spruce, and 25 open-pollinated families from each of six Cordova, Kenai Peninsula, Iniskin Peninsula, and

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[1] By definition, commercial forests in Alaska must grow at least 20 cubic feet of industrial wood per acre annually.

not fully analyzed, and the results have not been reported in the technical literature (pages two and three). Resolution of the genetic structure of the spruce complex requires both extensive and in-depth (intensive) research. Funds were inadequate to complete all studies scheduled in Appendix III of the Grant Agreement (page 6), and technical support and operating budgets were not allocated by the U.S. Forest Service as anticipated. In addition, support from an U.S. Forest Service and U.S. Navy cooperative agreement was reduced in fiscal year 1990, and the agreement was not renewed in fiscal year 1992.

Plans to prepare technical reports on results of the family heritability, and wide-range provenance studies (nursery studies one and two of the grant agreement), and the allozyme analyses hinge on funds and technical support for a quantitative or population geneticist position at the University of Alaska or the Institute of Northern Forestry in 1994 and 1995. Because Sitka spruce from southern and eastern latitudes is larger and may grow faster than Sitka spruce from northern and western latitudes, results of the wide-range provenance studies in the nursery and field are of major interest to the land owners and cooperators in the research. The results of nursery studies one and two are needed to guide future tree breeding programs, and the allozyme analyses are necessary to determine the extent of natural hybridization, to delineate breeding zones, and prevent losses from maladaptation of planting stock.

To continue the research initiated by grant agreement 89-1-015, and support quantitative, population and ecological genetic research positions in the private sector or at the University of Alaska and Institute of Northern Forestry, and to initiate afforestation and tree improvement programs for improving forest productivity and biodiversity in Alaska, research greenhouses and laboratories are needed for biochemical genetics research and seed and vegetative propagation. These facilities and research positions are necessary to elucidate the population structure of the spruce complex, establish breeding zones, and determine the crossability among hybrid species, the stability of populations and selected genotypes in changing environments, the size of breeding populations and zones, and the genetic gain from selection of desirable traits. Applied research is also needed to improve vegetative propagation technologies, induce early flowering of tree species, and accelerate tree breeding and the production of genetically improved seed.

If the procedures outlined on pages nine and ten of this report are put into practice by the land owners and cooperators in this research, the results in Table 1 and discussions on pages seven and 25 to 27 indicate that seed of tested families and parents established at random in seedling or grafted seed orchards will grow about 20 percent taller, 15 percent larger in diameter, and produce fewer basal knots and shorter branches than seed of

parents selected at random in wild populations. These results also support the forest genetics research and tree improvement programs summarized in the above paragraph and proposed in "Tree Improvement, Nursery and Research for Interior and South Central Alaska[2]."

[2] "Tree Improvement, Nursery and Research for Interior and South Central Alaska" is a report initiated by U.S. Senate Conference Report 102-256 of the fiscal year 1992 Appropriation Committee for the Department of Interior and Related Agencies, sponsored by the Alaska Department of Natural Resources, Division of Forestry and the Alaska Reforestation Council, and compiled by John Scholtes, U.S. Forest Service, Anchorage, Alaska, May, 1992.

GENETIC DIVERSITY IN THE SPRUCE COMPLEX OF COASTAL ALASKA
Final Report for ASTF Grant Agreement 89-1-015

EXECUTIVE SUMMARY

Background

During the late twentieth century, annual timber harvest in south central and southwest Alaska increased from a few million board feet before 1986 to more than 130 MBF in 1991.[1] Forest regeneration can be unsatisfactory under the conditions of accelerated timber harvest because the best stands and trees are often removed, leaving inferior trees to regenerate the new forest. If regenerated with genetically-improved seed, however, second-generation forests will be more productive than the virgin forests they replace.

The basic and applied genetic research undertaken in this project was directed at improving the growth and wood quality of the second-generation spruce forests of coastal Alaska. We investigated the genetic variation in adaptability, growth, and wood quality of the coastal spruce complex in order to determine selection responses for tree improvement and harvest indexes for future forest industries.

The Sitka and Lutz spruce (the natural hybrid of Sitka and white spruce) forests of south central and southwest Alaska are inferior to the Sitka spruce forests of southeast Alaska with respect to tree growth, wood quality, and stem volume. Sitka spruce migrated to Prince William Sound only 3,000 years ago, and stands in southwest Alaska are first-generation arrivals often less than 200 years old. This project investigates whether the inferior growth and wood quality of the northern coastal forests of south central and southwest Alaska might be caused by "bottleneck effects" of rapid migration and small founder populations, rapid natural selection for wind, cold soils, and climate, or by white spruce introgression.

Objectives

The overall research objective of this project was to resolve the genetic structure and variation in the spruce complex of the coastal region of Alaska, including the extent of hybridization and introgression in the Sitka, white, and black spruce complex, genetic variation within and among populations, and the rate and

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[1] "Timber supply and demand in southeast Alaska," ANILCA Section 705(a) Report to Congress - Fiscal Year 1991, USDA Forest Service, Alaska Region, Juneau, Alaska. 21 pgs.

direction of Sitka spruce migration. We also investigated possible "bottleneck effects" on genetic variation in growth, wood quality, tree form, and adaptability of the Sitka spruce forests in south central and southwest Alaska.

Common environment studies were established in the nursery and field to test the null hypotheses (1) that genetic variation in growth and wood-quality traits within and among provenances of south central and southwest Alaska is zero and gain from selection is not possible, and (2) that wood yield and quality, and adaptability of widely-separated provenances from central British Columbia to southwest Alaska, are equal.

In support of the common environment studies, basic research objectives were to determine the migration rate and direction of gene flow in the north coastal spruce complex (allozyme[2] research) and the extent of hybridization and introgression among the spruce species (by DNA fragment analysis). Basic and applied research objectives are outlined in the Technical Report, Part III.

Methods

Basic research:

Genetic differentiation among and within coastal spruce populations was investigated in a series of allozyme variation and species-specific chloroplast DNA marker studies to estimate evolution and migration rates of Sitka spruce, and to determine the extent of hybridization and introgression of Sitka, black, and white spruce in coastal Alaska.

Seed of about 30 trees in each of seven Sitka spruce populations from Kodiak Island to Mitkof Island in southeast Alaska, and 18 populations from the Sitka and white spruce hybridization and introgression zone of south central and southeast Alaska were analyzed for allozyme variation. Indexes of genetic variation, inbreeding, migration rate and direction were derived from the allozyme frequencies, and were related to genetic differentiation and geographical distances among populations.

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[2] An enzyme can have two or more forms termed "allozymes," distinguished by differences in amino acid sequence. Allozymes are the first products of the genes (alleles) of an organism and their messenger-RNA. Variation in the amino acid sequence results from a change or mutation in the DNA base pairs which code for the enzyme. In an electric field, allozymes of an enzyme will migrate at slightly different rate because of slight variation in their molecular form, size, and charge.

heterozygosity (H) decreased, while rare alleles and inbreeding increased from southeast to southwest Alaska.[3] Populations from Kodiak and Afognak Islands were more closely related to southeast populations on Mitkof Island and the Haines Highway than to populations on Kenai Peninsula. Genetic distances were not related to geographic and coastal distances between populations. Genetic variation (P=0.85, alleles per locus=2.00, H=0.18) of Sitka spruce in southwest Alaska was above average for conifers, and indicated that tree growth, form, and adaptability (vigor) can be improved by selecting and breeding the best genotypes.

Allozyme variation of Sitka and white spruce introgression in and among the 18 populations studied in the broad region of species overlap (sympatric region) in south central Alaska has only been partially analyzed and the results are not available at this date.

An examination of chloroplast DNA markers showed that DNA fragment polymorphisms are reliable markers for monitoring gene flow and identifying species, that interspecific hybridization occurs in regions where Sitka and white spruce overlap, and that species-specific DNA markers support morphological evidence of unrestricted gene flow between sympatric populations of Sitka and white spruce (Sigurgeirsson et al., 1990). Furthermore, species-specific chloroplast DNA markers showed that small amounts of white spruce DNA were present throughout the coastal Sitka spruce zone in Alaska but not in British Columbia. In contrast, Sitka spruce chloroplast DNA was not found in any of the pure white spruce populations sampled in south central Alaska (Sigurgeirsson et al., 1992).

Detail of the basic research cited above is reported in:

Sigurgeirsson, Adalsteinn, Alfred E. Szmidt and John N. Alden. 1990. A Molecular Study of Interspecific Hybridization in the Spruce Complex of Alaska. In: Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties S2.02-05, 06, 12 and 14, Douglas-fir, Contorta pine, Sitka Spruce, and Abies Breeding and Genetic Resources. Olympia, WA, USA. August 20-24, 1990. Sponsored by Weyerhaeuser, Forest Resources/Strategic Biological Sciences Technology Center, Tacoma, WA, USA 98477 Pgs. 6.14-6.23.

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[3] "Locus" is the position or location of the genes ("alleles") on homologous chromosomes; "polymorphism" is the frequency of loci with two or more genes (i.e., alleles); and "heterozygosity" is the frequency of loci with two or more alleles averaged over all individuals in a population.

Sigurgeirsson, Adalsteinn, Xiao-Ru Wang, John N. Alden and Alfred E. Szmidt. 1992. Patterns and extent of chloroplast gene exchange among Picea species in Alaska and British Columbia. In: Insights into the evolution of Picea inferred from chloroplast DNA. A Dissertation, Swedish University of Agricultural Sciences, Faculty of Forestry, Department of Forest Genetics and Plant Physiology, Umeå, Sweden 45 Pgs.

Applied Research:

The common-environment studies at the Alaska Regeneration Center demonstrated that

1. Seedlings of mainland Lutz spruce populations emerged sooner after sowing, grew faster, and ceased growth earlier at the Alaska Regeneration Center, Eagle River, than seedlings of the Sitka spruce populations from Kodiak and Afognak Islands of southwest Alaska. Height of the southwest Sitka spruce seedlings was not statistically different from the height of the mainland Lutz spruce seedlings after the first growing season, but they sustained statistically ($p<0.05$) more winter injury and mortality than the mainland Lutz spruce seedlings.

2. Genetic variation of Sitka spruce in south central and southwest Alaska was above average for conifers in general and indicated that tree growth, form, and adaptability (vigor) can be improved by selecting and breeding the best genotypes. Differences among one-year-old open pollinated families for each of five quantitative growth and wood-quality-related traits were significant at $p<0.05$ for each of six geographic regions (provenances) (Table 1). Sitka spruce families from south central Alaska (i.e., Cordova) grew faster and were taller, but did not have significantly more branches per basal stem unit than Sitka spruce families from southwest Alaska. These results indicate that slow height growth and not the number of branches per se may cause the inferior wood quality of southwest populations.

3. Growth of Sitka spruce from Kodiak and Afognak Islands was negatively correlated with altitude of the seed source. Height and stem diameter of one- and two-year-old seedlings decreased about nine percent per 100 meter increase in elevation of the seed parents.

4. Phenotype of the seed parents was largely an expression of the environment and had little predictive value for early offspring performance. As one-year-old seedlings, families of below average seed parents grew longer and faster, and were significantly ($p<0.05$) taller and larger in diameter than families of above average and plus-tree seed parents.

TABLE 1. GENETIC GAINS PREDICTED FOR GROWTH AND WOOD QUALITY TRAITS OF 1-0 SEEDLINGS IN THE SPRUCE COMPLEX OF COASTAL ALASKA

Region (provenance)	Family Mean[1] (cm)	Percent Gain Family Selection[2]	Percent Family Variance[3]	Heritability		Percent Second Generation Gain Selection Method[4]			
				Individual	Family	Family	Tree w/in Family	Total	Mass
October	**Height (cm)**								
1. Iniskin	32.1[ab]	10.5	8.5	0.26	0.71	7.3	9.0	16.3	14.0
2. Kodiak	32.3[ab]	9.9	11.8	0.35	0.80	7.7	10.5	18.2	16.6
3. Afognak	32.7[ab]	10.2	9.4	0.28	0.75	6.5	8.2	14.7	12.9
4. Port Chatham	31.3[ab]	10.9	10.6	0.32	0.79	9.2	11.9	21.1	18.8
5. Ninilchik	27.9[b]	14.3	16.8	0.48	0.89	12.7	18.5	31.2	30.0
6. Cordova	36.4[a]	8.2	9.3	0.28	0.76	6.5	8.1	14.6	12.7
Mean		10.7				8.3	11.0	19.3	17.5
Stnd. Deviation		+/-2.0				+/-2.4	+/-3.9	+/-6.3	+/-7.0
June to October Height Growth (cm)									
1. Iniskin	25.3[ab]	10.3	6.8	0.20	0.67	7.2	8.3	15.5	12.8
2. Kodiak	26.5[ab]	10.3	9.8	0.30	0.76	7.7	9.8	17.5	15.4
3. Afognak	26.6[ab]	10.9	7.1	0.22	0.70	6.1	7.0	13.1	10.9
4. Port Chatham	24.9[ab]	13.0	9.2	0.28	0.77	9.5	11.7	21.2	18.4
5. Ninilchik	21.7[b]	16.1	16.3	0.49	0.88	14.9	22.1	37.0	35.0
6. Cordova	29.5[a]	8.8	8.9	0.27	0.75	7.2	8.8	16.0	13.8
Mean		11.6				8.7	11.3	20.0	17.7
Stan. Devaition		+/-2.6				+/-3.2	+/-5.5	+/-8.7	+/-8.8
Epicotyl (Stem) Diameter (mm)									
1. Iniskin	3.0[ab]	10.0	6.3	0.19	0.74	5.8	6.1	11.9	9.4
2. Kodiak	3.1[ab]	6.4	10.0	0.30	0.82	7.5	9.3	16.8	14.6
3. Afognak	3.1[ab]	9.7	7.2	0.22	0.71	5.7	6.6	12.3	10.2
4. Port Chatham	3.1[ab]	9.7	9.0	0.27	0.74	7.7	9.5	17.2	14.9
5. Ninilchik	2.7[b]	10.5	9.4	0.28	0.82	8.0	9.7	17.7	15.2
6. Cordova	3.2[a]	9.4	6.4	0.19	0.74	5.5	5.8	11.3	9.0
Mean		9.3				6.7	7.8	14.5	12.2
Stan. Deviation		+/-1.5				+/-1.1	+/-1.8	+/-3.0	+/-3.0

GENETIC GAINS PREDICTED FOR GROWTH AND WOOD QUALITY TRAITS OF 1-0 SEEDLINGS
IN THE SPRUCE COMPLEX OF COASTAL ALASKA

Region (provenance)	Family Mean[1] (cm)	Percent Gain Family Selection[2]	Percent Family Variance[3]	Heritability		Percent Second Generation Gain Selection Method[4]			
				Individual	Family	Family	Tree W/in Family	Total	Mass
Number of Branches									
1. Iniskin	3.7[a]	13.5	10.3	0.31	0.76	9.8	12.6	22.4	19.9
2. Kodiak	3.3[ab]	9.1	4.7	0.14	0.55	5.5	5.8	11.3	8.9
3. Afognak	3.1[b]	9.7	9.9	0.30	0.74	8.6	11.1	19.7	17.5
4. Port Chatham	3.5[ab]	17.1	18.2	0.54	0.84	16.3	25.8	42.1	42.1
5. Ninilchik	3.7[a]	11.4	6.5	0.19	0.61	6.8	8.0	14.8	12.4
6. Cordova	3.5[ab]	11.4	14.0	0.42	0.81	11.8	17.0	28.8	27.5
Mean		12.4				9.8	13.4	23.2	21.4
Stan. Deviation		+/-2.9				+/-3.9	+/-7.2	+/-11.1	+/-12.0
Length of Longest Branch (cm)									
1. Iniskin	8.3	24.1	15.4	0.46	0.84	18.1	26.8	44.9	43.2
2. Kodiak	9.3	14.0	5.9	0.18	0.64	7.3	8.1	15.4	12.5
3. Afognak	9.2	14.1	9.4	0.28	0.74	10.0	12.6	22.6	19.9
4. Port Chatham	7.9	17.7	9.6	0.29	0.74	12.5	15.9	28.4	25.0
5. Ninilchik	6.7	20.7	12.2	0.36	0.77	15.3	21.3	36.6	33.8
6. Cordova	9.7	15.5	8.8	0.26	0.73	10.9	13.5	24.4	21.1
Mean		17.7				12.3	16.4	28.7	25.9
Stan. Deviation		+/-4.0				+/-3.9	+/-6.7	+/-10.6	+/-11.0

1 Values with a common letter are not statistically different at $P<0.05$.
2 First generation gain from 0.2 selection (1 in 5) of open-pollinated families from the wild unselected population.
3 Family variance, within replications and environments, represents 1/3 of the additive genetic variance in the wild unselected population.
4 Gain predicted from 0.2 selection of open-pollinated families (1 in 5) and 0.02 individual tree selection (1 in 50) within the selected families, followed by seed production from random interpollination among the selections. For mass selection, gains are predicted for 0.02 selection within replications (Blocks) and random mating among the selections in seedlings or clonal seed orchards.

In addition, families of above average parents were not different from families of average and below average parents in summer height growth, October height, and number of branches per basal stem unit.

5. In hybrid swarms, trees dominated by Sitka spruce characteristics will produce faster-growing offspring than trees dominated by Lutz and white spruce characteristics. Classification of hybrids into five (or seven) form classes based on morphological characteristics and selection of Sitka spruce hybrid forms proved to be an effective method of improving tree growth and wood yield.

Results of the applied research are described in more detail under the Technical Report, Part III. As the applied research progressed, emphasis gradually shifted from monitoring short-term nursery studies to establishing long-term field experiments. Problems were encountered in over-wintering the study seedlings at Eagle River Nursery, and early frosts injured or killed many seedlings in the field. Provenances transferred from latitudes south of the nursery responded to the long days of summer and failed to develop adequate hardiness before late summer and early autumn frosts. Families killed from early frosts in 1990 were sown again in 1992 and were outplanted in field trials in August and September of 1992.

Plans are to prepare a technical report on results of the 1989 and 1990 family and provenance nursery studies that are summarized in the Technical Report, Part III. The planned report is for peer review and will be published as a research note. It will be followed by a paper on the wide-range provenance (genetic) variation in Sitka spruce at north coastal tree limits. Results from the test of hypothesis 2 will be pooled with results of a similar provenance study carried out at Petersburg, Alaska in 1985, and results from five 5- to 7-year-old field trials within and beyond natural spruce limits in south central and southwest Alaska. Errors in the analysis of allozyme variation in the spruce complex must be corrected before the final report on results of the basic research is completed.

The ultimate success of the project depends on the availability of funds to maintain my position at the Institute of Northern Forestry in Fiscal Year 1994. Resolution of the genetic structure of the spruce complex was an extremely ambitious project at the onset and could only have been completed if each study was accomplished without delay or failure. Resources necessary to complete all of the research attempted were underestimated and funds requested were inadequate to complete the project as scheduled.

Results to date, however, support a modest tree improvement program for regenerating local spruce forests in coastal Alaska.

Assuming that genetic variation in seedling growth and traits related to wood quality remain stable until the new forests mature, parent evaluation and tree breeding programs at 0.2 selection of open-pollinated families will average 10 percent gain in growth and 12 to 18 percent gain in wood quality related traits for the first generation, and an additional 10 percent gain for the second generation (Table 1). Additional gains in northern and western coastal forests may be achieved from seed of fast-growing provenances in southeast Alaska. Improved forest yield and wood quality will increase Alaska's share of foreign and domestic markets for wood products and create jobs for the citizens of rural communities.

PART II. TECHNOLOGY TRANSFER

Research goals and bench marks

On completion of the data analysis and reports described above, all major research goals will be accomplished. Problems that arose during the course of the investigation necessitated some changes in the proposed experimental procedures:

1. Failure of seed collections from putative black x Sitka spruce hybrids to germinate precluded DNA fragment and allozyme analyses to confirm black and Sitka spruce hybridization and introgression in the coastal spruce complex, and to evaluate hybrid performance.

2. Early frost and winter injury at Eagle River Nursery in 1989 and 1990 prevented an assessment of phenology and growth during the second growing season. Frost injuries and other nursery effects may affect the field trials as well.

3. The common environment studies conducted at the nursery were designed to test the stability of regions, populations in regions, and families in two environmental extremes, i.e., in the greenhouse and outdoors. Differences between the greenhouse and outdoor environments were insufficient to cause genotype x environment interactions, and the stability of family and population performance was not tested.

4. Record low temperatures in late September 1992 and injuries from early frosts in 1990 may have introduced error in the long term field trials. As an alternative to the nursery project, it is proposed to sow seed directly on prepared microsites (planting spots) in the field to eliminate nursery effects.

During the investigation, research emphasis gradually shifted from short-term common garden studies in the nursery to long-term common garden studies in the field (Figure 1). Because results of the field studies will not be conclusive until the trees mature, accomplishments did not exceed the applied research outlined in the grant agreement. A major spin-off of the field trials was unexpectedly rapid growth of the nursery seedlings relative to natural regeneration in a 1990 outplanting at Two-Moon Bay. From the growth rates of both sources of regeneration, plans are to determine if, in the long run, growth and survival of artificial regeneration exceeds the growth and survival of pre-established natural regeneration.

Figure 1. An oblique aerial view of a field test site at 4.5 mile Main Road from Two Moon Bay in Port Fidalgo, Prince William Sound, Alaska. The site was logged in 1991 and the logging slash was piled in August 1992. A local family variation study was planted between the slash piles southeast (left) of the Loop Road and a wide-range provenance study was planted in the loop from August 25 to August 29, 1992.

Financial effects

No matching funds or in-kind support were secured during the grant period other than contributions by the cooperators outlined in the Grant Agreement ASTF 89-1-015. The US Navy provided funds for the seed collections, the Alaska Division of Forestry and US Forest Service produced the seedlings for the nursery and field experiments, and the Native Corporations provided the sites and established the field experiments. No follow-on support is in place or being sought at this time.

Under Collection Agreement Number PNW 92-0127 between Citikon Forest Products Inc., Anchorage, Alaska and the US Forest Service, Pacific Northwest Research Station, Portland, Oregon, $3668.84 was transferred to a Forest Service Account Number 632281 on January 31, 1992. The funds were expended from 6/13/92 to 8/20/92 for maintaining and packaging the seedlings and for layout, planting, and mapping field trials. The field trials were established at Cordova (Two Moon Bay and Sheridan Glacier) from 8/25/92 to 9/03/92 and on Afognak Island from 9/13/92 to 9/22/92 with the following expenditures from account number 632281:

Airfare	
Three, Fairbanks to Anchorage and Return	$ 478
Two, Fairbanks to Cordova and Return	1,100
Two, Fairbanks to Kodiak and Return	808
Total Airfares	$2,386
Per diem and car rentals	$1,320
Salary	
D. Vachitis: 58 hours at $13.93/hour	$808
Total project expenditures for 1992	$4,515
Project deficit covered by USFS accounts	<$845>

Implementation of the results

Results of the common environment studies show that Sitka spruce is highly variable. If the genetic variation demonstrated among the seedling families within provenances in this study is equivalent to the variation within the second generation populations (provenances) at maturity, then the potential genetic gain in the spruce complex of coastal Alaska is adequate for a profitable tree improvement program. The potential genetic gains demonstrated for Sitka and Lutz spruce by this research support ASTF proposal "A Tree Improvement Program for Alaska" submitted April 10, 1992.

The following procedure is recommended for improving the growth and wood characteristics of coastal Sitka and Lutz spruce:

1. For each commercial species, establish breeding zones[4] for the geographic region in need of reforestation with improved seed or other propagules.

2. Select at least 100 phenotypes (three to five per thousand acres of commercial forest land).

3. Progeny test open-pollinated seed in nursery and field experiments. Bulk the seed from the best 20 to 25 families for immediate reforestation. This is the first generation gain in wood yield and quality.

4. Establish a series of long-term field trials and select the best families followed by the best trees within families to produce the seed or propagules for the second generation of improvement.

These steps are being initiated for Sitka and interior white spruce under ASTF Grant Proposal 92-2-082, "A Tree Improvement Program for Alaska." After the evaluation trials for the initial selections are established, landowners will maintain the selections and trials, establish breeding or seed zones, select the second generation parents of breeding and seed producing populations, and establish breeding orchards for the third generation of improvement.

Economic impact on Alaska

Results of the research show that if applied immediately, selection of one in five open-pollinated families (0.2 intensity) for the first generation of tree improvement will increase the height and diameter of 1-0 (first-generation) seedlings an average of 10 and 9 percent, respectively (Table 1). First generation family selection at 0.2 intensity will also reduce the number of branches of 1-0 seedlings 12 percent and length of the longest branch 18 percent. Assuming that the gains will hold until harvest, forests regenerated with improved planting stock will be far more productive and create more jobs for citizens of rural communities than forests regenerated with conventional planting stock. Improved forest yield and wood quality will enable Alaska's forest products industry to capture a larger share of the domestic and foreign markets for wood products.

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[4] Breeding zones are geographic regions of similar environment into which an improved population of adapted trees will be introduced.

PART III. TECHNICAL REPORT

Objectives

To resolve the genetic structure and variation in the spruce complex of coastal Alaska in support of applied research and tree improvement, basic research objectives were to:

1. Assess the amount and geographic distribution of genetic variation, and to estimate evolution and migration rates, and direction of migration of Sitka spruce in the Gulf of Alaska.

2. Estimate the extent of hybridization and introgression in the spruce complex, and the direction of gene flow (Sitka into white spruce, or white into Sitka spruce).

3. Estimate genetic divergence among and within Sitka spruce populations.

Figure 2. Phenotypic variation in crown size of Sitka spruce from Pillar Road, Kodiak Island. The distance between branch whorls and stem volume of knot-free wood are reduced by the slow height growth of southwest populations.

Applied research objectives were to:

1. Demonstrate increased tree growth from introgression of Sitka spruce in white spruce in south central Alaska.

2. Demonstrate genetic variation in survival, growth, and wood-quality-related traits (Figure 2), and estimate gains from tree improvement.

3. Identify superior seed sources or provenance regions for reforestation and afforestation in south central and southwest Alaska.

Methods

Open-pollinated seed was harvested at random from 30 to 60 trees selected at random in twenty-five populations (geographic sources or provenances[5]) in southwest and south central Alaska from 1987 to 1990 (Figure 3). Elevation above mean sea level was documented for each seed tree. For 1990 collections, seed trees were classified as below average, average, above average, and "plus-tree" in size and form, or phenotype[6] (Figure 4). Seed trees of Sitka x white spruce hybrid swarms were classified into the two pure species and three hybrid forms (Sitka x Lutz, Lutz, and white x Lutz) based on morphological characteristics resulting from hybridization and introgression of one species into another. Basic research methods are summarized the Executive Summary, Part I of this report.

Applied research:

Genetic variation and gain from selection of quantitative traits (i.e., growth) were investigated in a series of common environment studies at the Alaska Forest Regeneration Center, Eagle River, Alaska.

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[5] Provenance is the original geographic location or source of seed delimited by similar environment; population refers to a group or stand of related individuals (usually interbreeding) delimited by a common environment or provenance.

[6] Phenotype is the state, description or degree of expression of a character as it appears to us; or the product of the interaction between the genes of an organism (genotype) and the environment. The phenotype describes the individual when all characteristics (traits) are considered.

Figure 3. Timber harvest in Section 10, T16S, R1W near Sheridan Glacier, Cordova, Alaska on September 21, 1989. Seed was collected from felled trees selected at random in the sale area (60° 30' N. Lat., 145° 23' W. Long.).

Seed of 12 trees (families) for each of ten geographic areas (provenances) in the Sitka and Lutz spruce regions of southwest and south central Alaska were replicated in a common environment (greenhouse) study in 1989 to characterize variation in growth, phenology (timing of onset and termination of growth and dormancy), and winter hardiness. Differences among mainland and Kodiak-Afognak island regions, among provenances (populations) within regions, and among trees (genotypes) within provenances were tested by analysis of variance (ANOVA). Growth, winter hardiness, and phenology, measured as dates of bud burst and bud set, were related to altitude of the seed parents.

In 1990, open-pollinated seed of 25 families each for Cordova, Port Chatham, Iniskin Peninsula, Ninilchik, Afognak, and Kodiak populations (provenances) were also sown in a replicated common garden study to estimate first and second generation genetic gains from artificial selection of seedling growth and wood-quality-related traits (quantitative traits) in wild populations (Figure 5). First generation gains were estimated for stem height, height growth, epicotyl diameter, reduction in branch number in a 2.5 centimeter stem unit from the cotyledons, and

branch length from selection of the best one-year-old (1-0) seedling family in five families (0.2 selection intensity). Second generation gains were estimated for combined family and within family selection of 1-0 seedlings at intensities of 0.2 and 0.02 (best within family seedling among 50 seedlings) respectively, and for mass selection at 0.02 intensity followed by random matings among the selections in general combining seed orchards or plantations. Second generation gains were also estimated for 1-0 seedling height, June to October height growth, epicotyl diameter, and reduction in branch number and length. Distribution of data for important traits such as frost injury, position of the largest branch on the stem (crown form) and bud set were not continuous. Traits with discontinuous data were tested for differences among populations by nonparametric statistical methods.

Figure 4. Seeds were collected from residual trees selected at random at Port Chatham, Kenai Peninsula (59° 13' N. Lat., 151° 46' W. Long.) on September 15, 1989. The area was harvested in the mid 1970's. Only 29 percent of the residual seed parents were above average phenotypes. Fifty-eight and 13 percent of the seed parents were below average and average phenotypes, respectively. No plus trees were sampled in the harvested area.

Figure 5. Sitka and Lutz spruce seedlings in four completely randomized blocks of 150 families and seven tree plots each from six regions (provenances) in an outdoor environment at the Alaska Regeneration Center, Eagle River, Alaska in August, 1990.

In a provenance experiment, bulked seed from each of 45 wide-range provenances at 30 minute intervals of latitude from central British Columbia to Kodiak Island were sown in replicated common environment studies to assess differences among distant populations in growth, phenology, hardiness and wood-quality-related traits.

Finally, seedlings from both the 1990 family and wide-range provenance experiments were transplanted from the nursery to four sites in the coastal Sitka spruce zone. Data from long-term field experiments will confirm or refute results of the short-term nursery studies, reveal differences among populations and families in growth, tree form and vigor, provide juvenile-mature correlations for quantitative traits, and reveal genetic gains from selection and tree breeding within local populations.

Experimental design and analysis of data:

To test the null hypotheses that genetic variation in growth and wood quality within and among local regions (locations or provenances) is zero, and that the wood yield and quality, and adaptability of wide-range provenances are equal, nursery experiments were designed with the above seed collections for

testing differences among locations, populations (provenances) in locations, families in provenances and locations, and for testing environment x location, environment x population, and environment x family interactions. Four blocks of seven tree plots for each open-pollinated family were grown outdoors and in a greenhouse from June to October. Variation among populations and families in June seedling height, October seedling height, and October bud set in 1989 were subjected to analysis of variance:

Source of Variation	df	ms	F	p
Environment	1			
Replication (Environment)	6			
Location	2			
Provenance (Location)	7			
Environment x Location	2			
Environment x Provenance	7			
Replication x Location	12			
Replication x Provenance	42			
Family (provenance)	110			
Environment x Family(Provenance)	110			
Replication x Family(Provenance)	660			
Error	5760			
Total	6719			

Where df=degrees of freedom;
ms=mean square;
F=a test statistic derived from a distribution of variance ratios, and used to determine if two sample variances are from the same population;
p=probability that the two variances are from the same population.

Seedlings grown in the greenhouse in 1989 failed to harden and were winter killed in 1989-90. During 1990, winter injury, date of terminal and lateral bud burst, October 1990 height, hypocotyl diameter and condition, and 1989 and 1990 height growth (October height minus June height) were measured for each seedling in the outdoor environment.

The relationship between altitude of seed parent and family performance was examined by SAS linear regression analysis with second and third order models for best fit (Figure 1).

For the 1990 sowing, June height, October height, height growth, October epicotyl diameter, number of branches, and branch length were subjected to ANOVA for significance of differences among regions, populations in regions, and families:

Source of Variation	df	ms	F	p
Environment	1			
Replication (Environment)	6			
Region	5			
Population (Region)	5			
Environment x Region	5			
Environment x Population	5			
Replication x Region	30			
Replication x Population	30			
Family (population)	139			
Environment x Family (population)	139			
Replication x Family (population)	834			
Error	7200			
Total	8399			

Distribution of data for crown form (position of the longest branch on the stem), early frost injury, and percent bud set in October were not normal, and differences among regions, populations, and families were tested with non-parametric statistics.

Differences among populations within regions were not statistically significant ($p<0.05$) for each variable examined. For this reason, variation due to populations was pooled with variation among families within regions. Variance components were then estimated for each growth and wood-quality-related variable within regions by a SAS General Linear Model Varcomp Procedure:

Source of variation	DF	Expected mean square
Family	24	Var(error) + NVar(Rep*Fam) + NRVar(Fam*Envir) + NFVar(Rep(Envir)) + NRFVar(Envir) + NREVar(Fam)
Environment	1	Var(error) + NVar(Rep*Fam) + NRVar(Fam*Envir) + NFVar(Rep(Envir)) + NRFVar(Envir)
Rep(Environment)	6	Var(error) + NVar(Rep*Fam) + NRVar(Fam*Envir) + NFVar(Rep(Envir))
Environment x Family	24	Var(error) + NVar(Rep*Fam) + NRVar(Fam*Envir)
Rep x Family	144	Var(error) + NVar(Rep*Fam)
Error	1200	Var(error)
Total (corrected)	1399	

Where N=harmonic mean number of trees in plots;
R=number of replications (blocks) per environment;
E=number of environments;
F=number of families.

From the variance components above, heritabilities and genetic gains for growth and wood-quality-related traits of 1-0 seedlings were determined for family, within family, and mass selection at 0.2 (family) and 0.02 (within family and mass) intensities after the procedures of Namkoong et al. (1966) and Shelbourne (1969).[7]

Family variance was assumed to represent one-third of the additive genetic variance within populations:

Var(Fam)=1/3Var(A)

Genetic gain was estimated as follows:

Genetic Gain=i*Var(A)/Phenotypic standard deviation (population)

Genetic gain from family selection=i*Var(Fam)/
[Var(W)/NRE+Var(Rep*Fam)/RE+Var(Fam*Evir)/E+Var(Fam)]$^{1/2}$

Genetic gain from individual selection within families=
i*2Var(Fam)/[Var(W)+Var(Rep*Fam)+Var(Fam*Evir)+2*Var(Fam)]$^{1/2}$

Genetic gain from mass selection=
i*3Var(Fam)/[Var(W)+Var(Rep*Fam)+Var(Fam*Evir)+Var(Fam)]$^{1/2}$

Heritabilities for additive genetic variation (Narrow Sense):

Individual heritability:

h_i^2 =Var(A)/Var(P)=3Var(Fam)/[Var(W)+Var(Rep*Fam)+Var(Fam*Evir)
+Var(Fam)]

Family heritability:

h_f^2 =Var(Fam)/[Var(W)/NRE+Var(Rep*Fam)/RE+Var(Fam*Evir)/E
+Var(Fam)]

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[7] Namkoong, Gene, E.B. Snyder, and R.W. Stonecypher, 1966. Heritability and gain concepts for evaluating breeding systems such as seedling seed orchards. Silvia Genetica 15(3):76-84.

Shelbourne, C.J.A., 1969. Tree breeding methods. Forest Research Institute, New Zealand Forest Service, Wellington, N.Z. Technical Paper No. 55. 43 pgs.

Where Var(A)=additive genetic variance;
Var(W)=within plot variance or Var(error);
i=selection intensity in units of standard deviation;
N=harmonic mean number of trees in plots;
R=number of replications (blocks) per environment;
E=number of environments.

Differences in growth and wood-quality-related traits among three hybrid form classes in Ninilchik region were tested with a SAS Analysis of Variance procedure:

Source of Variation	df	ms	F	p
Hybrid-form	2			
Family(Hybrid-form)	18			
Replication	7			
Hybrid-form*Replication	14			
Family(Hybrid-form)*Replication	126			
Error	1008			
Total	1175			

Differences among seed parent phenotypes were also tested for each growth and wood-quality-related trait with a SAS Analysis of Variance procedure:

Source of Variation	df	ms	F	p
Phenotype	3			
Replication	7			
Phenotype*Replication	21			
Error	3832			
Total	3863			

Results

The 1989 common environment study showed that mainland Lutz spruce populations grew faster after seed germination, but ceased growth and developed winter hardiness earlier at Eagle River Nursery than Sitka spruce populations from Kodiak and Afognak Islands. Seedlings of Kenai Peninsula and mainland Lutz spruce populations were not statistically taller (27.2 cm) than seedlings of Kodiak and Afognak Sitka spruce populations (26.1 and 28.5 cm, respectively) at conclusion of the first growing season.

Mainland Lutz spruce populations sustained statistically ($p<0.05$) less winter injury and seedling mortality than the Sitka spruce populations from Kodiak and Afognak Islands (eight vs thirty percent), initiated growth five days earlier, and ceased growth earlier at conclusion of the second growing season. Variation in two-year seedling height and diameter were significant for populations within the Island and mainland locations, and for families within populations but not for locations.

Growth was negatively correlated with altitude of the populations and seed parents within populations from Kodiak and Afognak Islands (Figure 6). As seed parents approached altitude tree limits from 200 to about 400 meters, first year seedling height declined in a second order relationship. Height of one- and two-year-old seedlings decreased 9.0 and 7.8 percent per 100 meter increase in altitude of seed parents from sea level to tree limits. Hypocotyl stem diameter of two-year-old seedlings also decreased 8.3 percent per 100 meter increase in altitude. Growth was positively correlated with speed of seedling emergence and number of seedlings that emerged per cell. Seed vigor, a maternal trait, is modified by the tree's environment, especially at tree limits, and can be a major source of error in estimating genetic variation in seedling growth characteristics.

Figure 6. Decline in height of one-year-old (OCTHT) and two-year-old (LASTHT) seedlings, and stem diameter (HYPODIA) of two-year-old seedlings from Kodiak and Afognak Islands with altitude of seed parents. Dashed lines about the regressions are 95 percent confidence limits for mean predicted values. The one-year-old seedling height and altitude of seed parent relationship was best described by the second order regression model (M2) below.

Model: M2
Dependent Variable: Height at one year (OCTHT).

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	2	540.47799	270.23899	24.927	0.0001
Error	79	856.44004	10.84101		
C Total	81	1396.91803			

Root MSE	3.29257	R-square	0.3869
Dep Mean	23.43817	Adj R-sq	0.3714
C.V.	14.04789		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob>¦T¦
INTERCEP	1	24.865933	0.87037756	28.569	0.0001
ALTITUDE	1	0.006855	0.01399506	0.490	0.6256
ALTSQUR	1	-0.000089798	0.00003943	-2.277	0.0255

Model: M1
Dependent Variable: Height at one year (OCTHT).

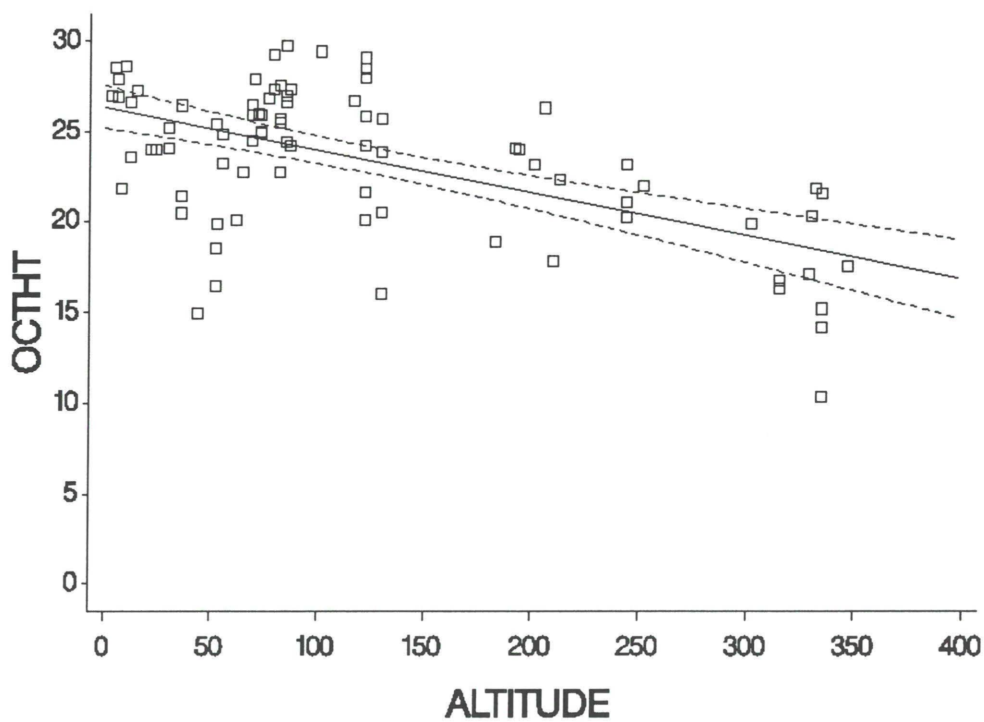
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	1	484.26025	484.26025	42.448	0.0001
Error	80	912.65778	11.40822		
C Total	81	1396.91803			

Root MSE	3.37761	R-square	0.3467
Dep Mean	23.43817	Adj R-sq	0.3385
C.V.	14.41071		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob>¦T¦
INTERCEP	1	26.365321	0.58393048	45.151	0.0001
ALTITUDE	1	-0.023952	0.00367635	-6.515	0.0001



October (1-0) height is in centimeters and altitude is in meters.

Model: M1
Dependent Variable: Two year height (LASTHT).

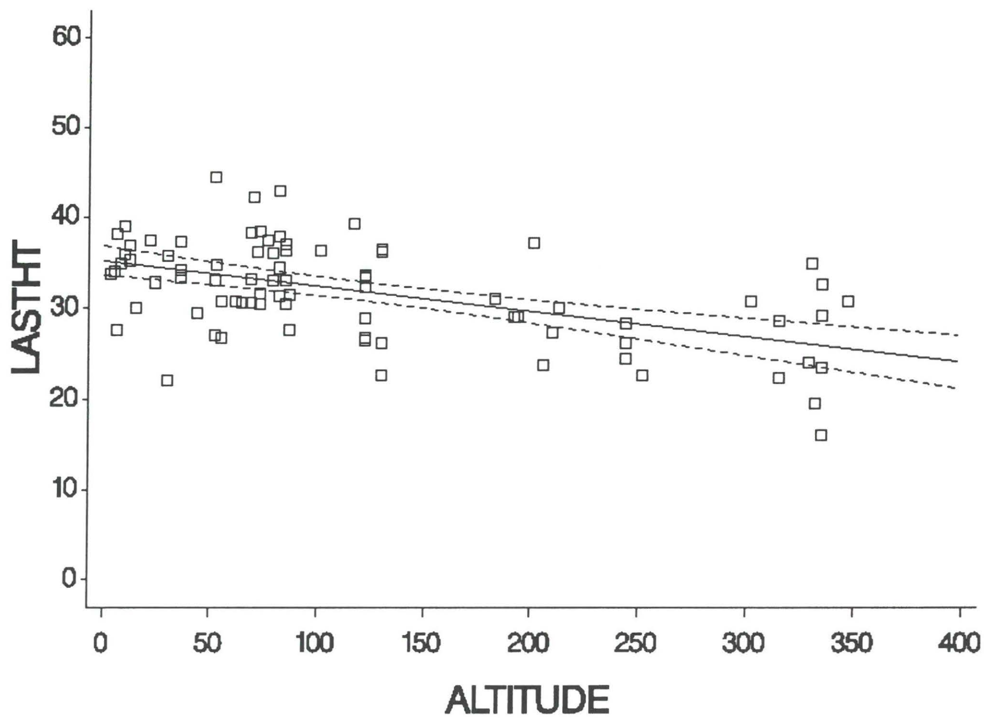
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	1	647.28041	647.28041	30.606	0.0001
Error	80	1691.87857	21.14848		
C Total	81	2339.15898			

Root MSE	4.59875	R-square	0.2767
Dep Mean	31.79951	Adj R-sq	0.2677
C.V.	14.46169		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob>|T|
INTERCEP	1	35.183679	0.79504508	44.254	0.0001
ALTITUDE	1	-0.027692	0.00500551	-5.532	0.0001



Last height (2-0) is in centimeters and altitude is in meters.

Model: M1
Dependent Variable: Stem diameter under the first needles or cotyledons (HYPODIA).

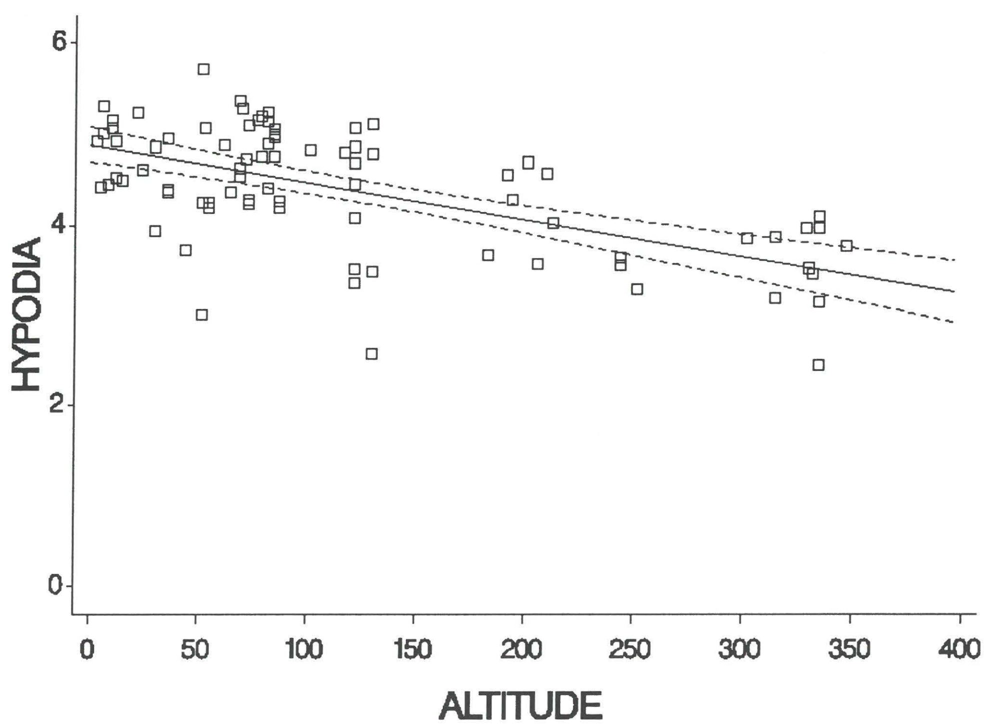
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	1	14.00377	14.00377	47.184	0.0001
Error	80	23.74346	0.29679		
C Total	81	37.74722			

Root MSE	0.54479	R-square	0.3710
Dep Mean	4.37854	Adj R-sq	0.3631
C.V.	12.44222		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob>¦T¦
INTERCEP	1	4.876306	0.09418444	51.774	0.0001
ALTITUDE	1	-0.004073	0.00059297	-6.869	0.0001



Hypocotyl diameter is in millimeters and altitude is in meters.

In the 1990 family-provenance experiment, differences among open-pollinated families for each of the five quantitative traits in each provenance (geographical region) from southwest and south central Alaska were significant at $p<0.05$ (Table 1). Families from Cordova were taller (36.4 cm), larger in diameter (3.2 mm) and grew faster (29.2 cm) than families from provenances on Kenai Peninsula and southwest Alaska. Families from provenances on Kenai Peninsula and southwest Alaska averaged 31.2 cm tall, 3.0 mm in epicotyl diameter, and grew 24.6 cm from June to October (Figure 7). Families from Ninilchik and Iniskin Peninsula had more branches (3.7) per stem unit than families from Afognak (3.1) but they averaged only 7.4 cm long. In comparison, the longest branch of Afognak and Cordova families averaged 9.2 and 9.7 cm, respectively.

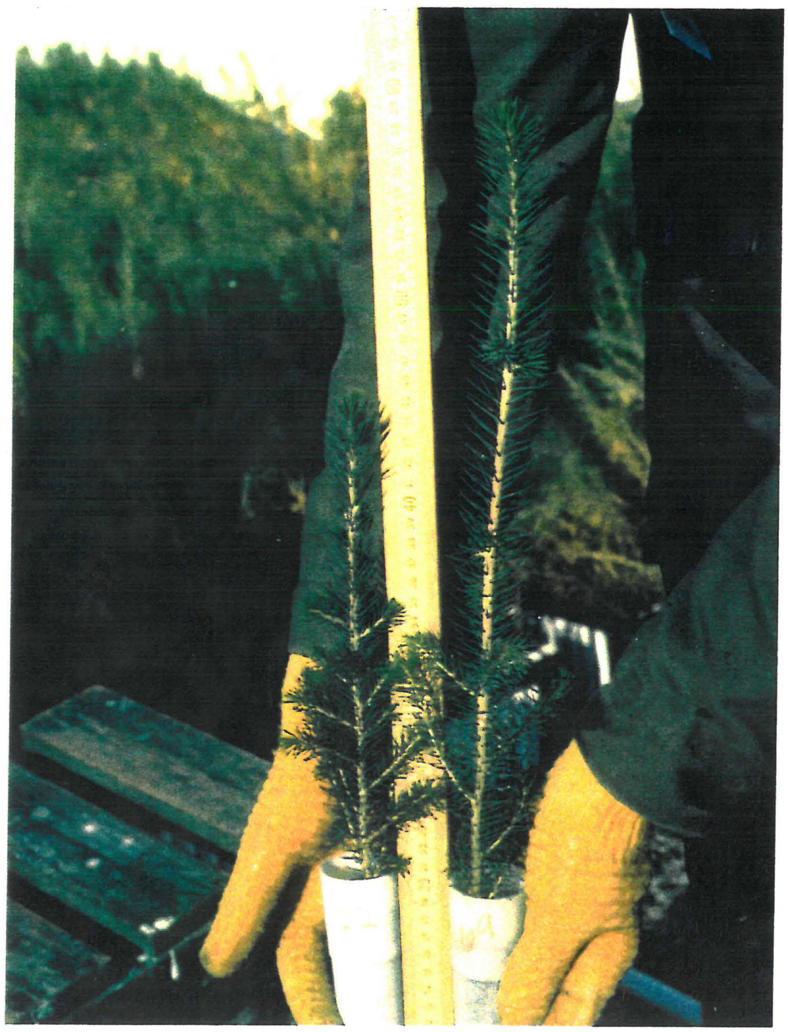


Figure 7. Variation in 1-0 height and branch characteristics among seedlings of families (Fam) from southwest Alaska. The Lutz spruce from Ninilchik (left, Fam 122) is 25 cm and the Sitka spruce from Afognak Island (right, Fam 69) is 38 cm tall.

Phenotypes were statistically different ($p<0.05$) for all quantitative traits under study. One-year-old families of parents with below average phenotype ceased terminal shoot growth later and were significantly taller (31.3 vs 30.7 cm) in October, grew faster in height (25.4 vs 24.6 cm), and were larger in diameter (3.1 vs 2.9 mm), than families of plus tree and above average parents combined. Families of above average parents were not different from families of average and below average parents in October height, summer height growth, and branch number. In addition, families of plus tree parents had more branches per stem unit than families of above average, average, and below average phenotypes. The stem diameter of plus tree families was smaller and their branches were shorter than families of average and above average parents, however. These results suggest that phenotype is largely an expression of the environment and reveals little about early offspring performance in common garden studies.

Hybrid form class, however, proved to be an effective method of classifying fast growing hybrids and introgression products for seed production and tree improvement. The Ninilchik hybrid population was genetically more variable and produced more gain from the same selection intensities than the pure Sitka spruce populations of the coastal forests (Table 1). Hybrid forms dominated by Sitka spruce were larger in stem diameter (2.8 vs 2.7 mm), grew faster (22.9 vs 20.4 cm), and were taller (29.2 vs 26.6 cm) than white spruce dominated hybrids after the first growing season. Thus in hybrid swarms, trees dominated with Sitka spruce characteristics will produce faster growing offspring than trees dominated by Lutz and white spruce characteristics. In addition, seedlings of the Sitka spruce hybrid form class averaged four percent larger in diameter, grew six percent faster in height from June to October, and were five percent taller than average seedlings in the Ninilchik population. The improved growth and seedling size of the offspring from the Sitka spruce hybrid forms provided nearly one-half of the genetic gain from 0.2 family selection shown in column 3 of Table 1. Four of the five fastest growing families were from the Sitka spruce hybrid form class. The fifth family was from the Lutz spruce form class.

The 1990 family-provenance study demonstrated that selection of the best one in five open-pollinated 1-0 seedling families (0.2 selection) within each of the six local provenances increased June to October stem growth 11.6 percent, and produced seedlings that were 10.7 percent taller and 9.3 percent larger in stem diameter than seedlings from un-selected wild populations (Table 1). Second generation genetic gain estimated from family and within family selection at 0.2 and 0.02 intensities, and followed by random mating in a general combining seed orchard or plantation, averaged 20.1 percent for June to October growth, 19.4 percent for 1-0 seedling height and 14.5 percent for

epicotyl diameter. Second generation gain from mass selection at 0.02 intensity, on the other hand, averaged 17.5 percent for 1-0 seedling height, 17.2 percent for height growth, and 12.2 percent for epicotyl diameter.

Number of branches per basal stem unit and length of the longest branch, which averaged 3.5 and 8.5 centimeters respectively, were reduced 12.0 and 17.7 percent at 0.2 selection intensity for the first generation. The quantitative procedures used to estimate second generation gain for family and within family selection and random mating among the selections reduced the number of branches per basal stem unit 23.2 percent and branch length 28.7 percent. Mass selection at 0.02 intensity reduced branch number and length 21.4 and 25.9 percent in the second generation. The number of branches and branch length of southwest populations (Afognak and Kodiak Islands) were not significantly different from those of south central populations (i.e., Cordova). These results suggest that slow height growth is responsible for the inferior wood quality of southwest populations and not the number of branches per stem unit per se. Thus wood quality can also be improved by selecting tall, fast growing families and trees within families to reduce stem taper and increase the clear wood between branch whorls.

Table 2. Pearson's linear correlation coefficients among growth and wood quality related variables. All relationships except epicotyl diameter and branch number are significant at less than 0.001 probability.

	Epicotyl diameter	October height	Height growth	Branch number	Branch length
Epicotyl diameter	----	0.66	0.62	0.00	0.53
October height		----	0.98	-0.10	0.57
Height growth			----	-0.10	0.53
Branch number				----	-0.16
Branch length					----

For all regions, growth traits were positively correlated with branch length (Table 2), and tall, fast growing and large diameter families will have large branches and crowns. To increase the harvest index[8] of the coastal spruce complex,

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[8] Harvest index is the proportion of biomass harvested relative to the total biomass of the plant.

populations improved for growth may require either additional selection, or breeding with populations selected for harvest index. Branch number, on the other hand, was not correlated with stem diameter, but was weakly correlated with October height and height growth (Table 2). The negative correlations between these relationships also indicate that the number of branches can be reduced and wood quality improved by selecting tall, fast growing families. These results support the above conclusion that slow height growth is responsible for the inferior wood quality of southwest populations.

The Cordova population had more (10.3 percent) and the Ninilchik population had less (0.3 percent) seedlings at $p<0.05$ with diamond shaped crowns (longest branch positioned near mid-stem). The Ninilchik and Iniskin Peninsula populations set bud earlier and sustained less winter injury than the coastal Sitka spruce populations from Kodiak, Afognak, Port Chatham, and Cordova.

CONCLUSION

The ASTF project "Genetic variation in the spruce complex of coastal Alaska" demonstrated that Sitka and Lutz spruce of south central and southwest Alaska are genetically diverse. Results of electrophoretic and common environment studies suggest that Sitka spruce migrated to southwest tree limits in large numbers and did not lose extensive genetic variation from bottleneck effects. Sitka spruce may have arrived in southwest Alaska before extensive hybridization and introgression of white spruce in south central Alaska.

Open-pollinated family and local provenance studies showed that (1) growth and wood-quality-related characteristics of 1-0 seedlings cannot be predicted from phenotype of the seed parents, (2) a Lutz spruce population from Kenai Peninsula was genetically more variable, and at the same selection intensity produced more gain than Sitka spruce populations from Cordova and southwest Alaska, (3) seedlings of the Lutz spruce population can be improved by selecting hybrid forms dominated by Sitka spruce characteristics, and (4) height and diameter growth of seedlings from southwest Alaska decreased about nine percent per 100 meter increase in altitude of seed source. Above 200 meters, growth decreased sharply with increasing altitude.

Variation in growth and wood-quality-related traits among open-pollinated families within populations (geographic regions or provenances) was highly significant. Height and stem diameter of one-year-old seedlings increased ten and nine percent, respectively, after one in five (0.2) selection of first generation open-pollinated families. Second generation gain in seedling height and diameter estimated from family and within family selection at 0.2 and 0.02 intensities was 19 and 14

percent, respectively. At the same selection intensities, branch number and length were reduced 12 and 18 percent after the first generation, and 23 and 28 percent after the second generation. Southwest populations (Afognak Island) grew less branches than mainland and east side (Cordova) populations, and number of branches was negatively correlated with height growth. These results indicate that wood quality can be improved by selecting families for both rapid height growth and less branches.